Revisiting the von Bertalanffy Seasonal Cessational Growth Function of Pauly et al. (1992)

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Introduction

The mean length-at-age for many animals (e.g., CITATIONS) is often modeled with the von Bertalanffy growth function (VBGF; von Bertalanffy (1938)). The parameterization of the VBGF attributable to Beverton and Holt (1957) is most common and may be expressed as

$$L_t = L_\infty(1 - e^{-q}) \qquad (1)$$

with

$$q = K(t - t_0) \qquad (2)$$

where $L(t)$ is the expected or average length at time (or age) t, L_∞ is the asymptotic mean length, K is a measure of the exponential rate of approach to the asymptote (Schnute and Fournier 1980), and t_0 is the theoretical time or age (generally negative) at which the mean length would be zero.

Many animals exhibit seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (CITATIONS). Equation 2 of the traditional VBGF has been modified, usually with a sine function, to model these seasonal oscillations in growth. The most popular of these modifications, from Hoenig and Choudaray Hanumara (1982) and Somers (1988), is

$$\begin{aligned} q =& K(t - t_0) \\ &+ \frac{CK}{2\pi}sin(2\pi(t - t_s)) - \frac{CK}{2\pi}sin(2\pi(t_0 - t_s)) \end{aligned} \qquad (3)$$

where C modulates the amplitude of the growth oscillations and corresponds to the proportional decrease in growth at the depth of the oscillation (i.e., "winter"), and t_s is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point). If C=0, then there is no seasonal oscillation and Equation 3 reduces to Equation 2 and the typical VBGF (Figure 1). If C=1, then growth completely stops once a year at the "winter-point" (WP), whereas values of 0<C<1 result in reduced, but not stopped, growth during the winter (Figure 1). Note that $WP = t_s + \frac{1}{2}$ because the sine function in Equation 3 has a period (i.e., the growth period) of one year. Some confusion has surrounded the use of Equation 3, though Garcia-Berthou et al. (2012) carefully clarified its form.

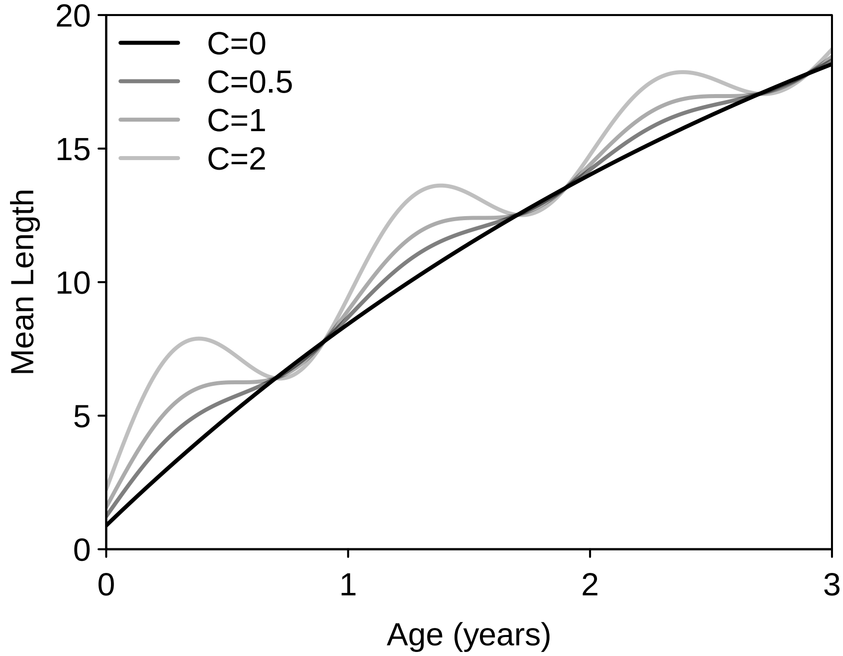

Figure 1: Example VBGF using Equation 3 with L_∞=30, K=0.3, t_0=-0.1, t_s=0.05 (with WP=0.55) and four different values of C.

Values of C>1 (or <0) in Equation 3 allow seasonal decreases in mean length-at-age (Figure 1). A decrease in mean length is unlikely for organisms whose skeletons largely preclude shrinkage (Pauly et al. 1992), although a seasonal decrease in mean length-at-age is possible if size-dependent overwinter mortality occurs (Garcia-Berthou et al. 2012). Pauly et al. (1992) modified Equation 3 to include a true seasonal no-growth period where mean length was not allowed to decrease and that included a smooth transition of the modeled mean length-at-age into and out of the no-growth period. Specifically, their modification is

$$\begin{aligned} q =& K^{'}(t^{'} - t_0) \\ &+ \frac{K^{'}(1 - NGT)}{2\pi} sin\left(\frac{2\pi}{1 - NGT}(t^{'} - t_s)\right) - \frac{K^{'}(1 - NGT)}{2\pi} sin\left(\frac{2\pi}{1 - NGT}(t_0 - t_s)\right) \end{aligned} \quad (4)$$

where NGT is the "no-growth time" or the length of the no growth period (as a fraction of a year) and $t^{'}$ is found by "subtracting from the real age (t) the total no-growth time occurring up to age t" (Pauly et al. 1992). Furthermore, Pauly et al. (1992) noted that the units of K changed from $year^{-1}$ in Equation 3 to $(1 - NGT)^{-1}$ in Equation 4. To eliminate confusion, they suggested using $K^{'}$ in Equation 4, as we do here.

Pauly et al. (1992) devised Equation 4 by assuming C=1 and replacing 2π with $\frac{2\pi}{1-NGT}$ (i.e., restricting the seasonal oscillation to the growth period and noting that $K^{'}$ only operates during the growth period). Their modification may be described geometrically (though not algorithmically) in two steps. First, the seasonal growth function with C=1 in Equation 3 is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using $t^{'}$). The growth trajectory is then separated at each WP and horizontal segments that are NGT units long are inserted at these points. This forms a growth trajectory that smoothly transitions into and out of the no-growth periods (Figure 2).

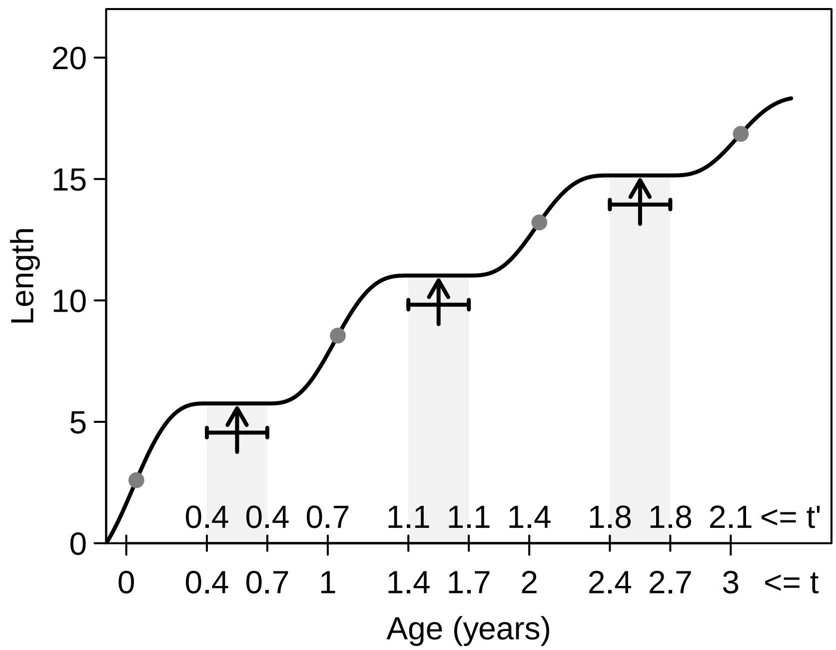

Figure 2: Example VBGF using Equation 4 with L_∞=30, $K^{'}$=0.35, t_0=-0.1, NGT=0.3, and t_s=0.05 (with WP=0.55). Each t_s is shown by a gray point, WP by a vertical arrow, and no-growth period by the horizontal interval centered on the WP arrow and the gray region that extends to the x-axis. The ages adjusted for the NGT (i.e., $t^{'}$) are shown above the x-axis.

Pauly et al. (1992) provided a "diskette" that contained a computer program to estimate the parameters of Equation 4. The diskette is difficult (at best) to obtain and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but there is no description of how $t^{'}$ was operationalized. This is an important step in using Equation 4 because $t^{'}$ is a function of t, but it is also a function of NGT and t_s, which are parameters to be estimated during the model-fitting process. Thus, the values for $t^{'}$ change with each iteration of the non-linear model-fitting process.

Therefore, the objectives of this note are to (i) operationalize the calculation of $t^{'}$, (ii) provide an (open-source) algorithm for the calculation of $t^{'}$ and Equation 4 for use in model fitting, and (iii) demonstrate the use of this algorithm.

Calculating $t^{'}$

As noted by Pauly et al. (1992) the calculation of $t^{'}$ depends on the observed age (t) and the cumulative no-growth time prior to t. In practice, the calculation of $t^{'}$ also depends on the position of the no-growth period within a year. Here, the position of the no-growth period will be defined relative to WP and NGT. The following algorithm may be used to convert from observed ages (t) to ages adjusted for cumulative NGT prior to age t ($t^{'}$).

1. Shift the age (t) by subtracting the start of the no-growth (SNG) period (i.e., $SNG = WP - \frac{NGT}{2}$) from t, such that a whole number will represent the start of a no-growth period. For example, if SNG=0.4, then t=2.4 will become 2.0 and t=2.9 will become 2.5.
2. Subtract the whole number age from the shifted age from Step 1 such that the remaining decimal represents the fraction of a shifted year. For example, a 0 will result if the shifted age is 2.0 and a 0.5 will result if the shifted age is 2.5.

3. Substract the NGT from the value from the previous step.
4. If the value from the previous step is negative, then the age is within the no-growth period and the negative value should be replaced with a zero. Otherwise, the positive value represents the amount of time into a growth period.
5. Add the value from the previous step to the total growth time completed (i.e., the product of the number of growth periods completed and the length of the growth period $(1 - NGT)$).
6. Compute t' by adding back the SNG that was subtracted in Step 1.

Further examples of $t^{'}$ values relative to t values are shown in Figure 2. This algorithm for computing $t^{'}$ is implemented in an R (R Development Core Team 2016) function as shown in Appendix 1. With this, Equation 4 is easly implemented as an R function as shown in Appendix 2.

Fitting the Function

Simulated Data

Simple simulated data are used initially to demonstrate the fitting of Equation 4. The data were simulated by randomly selecting 200 real numbers from a uniform distribution between 0 and 5 to serve as observed ages, plugging these ages into Equation 4 to compute a mean length for each age, and then adding a random deviate from a normal distribution with a mean of 0 and a standard deviation of σ to each mean length to simulate observed individual lengths. Eight data sets were simulated for all combinations of "early" ($t_s = 0.2$) and "late" ($t_s = 0.8$) maximum growth points, "short" ($NGT = 0.2$) and "long" ($NGT = 0.5$) no-growth periods, and "low" ($\sigma = 0.3$) and "high" ($\sigma = 0.5$) individual variabilities.

The `nls()` function from R was then used to estimate parameter values for the nonlinear Equation 4 fit to each simulated data set. The "port" algorithm was used so that L_∞ and $K^{'}$ could be constrained to be positive and t_s and NGT could be constrained to be between 0 and 1. The estimated parameters for each data were consistently very close to the values used to create the data set, with the possible exception of t_0. One example, for a "long" NGT, "late" t_s, and low individual variability, is shown in Figure 3. The results from fitting Equation 4 to these data sets are not surprising as one would expect the parameter estimates to be very close to the values used to create them, given that Equation 5 was used to both create and fit the data.

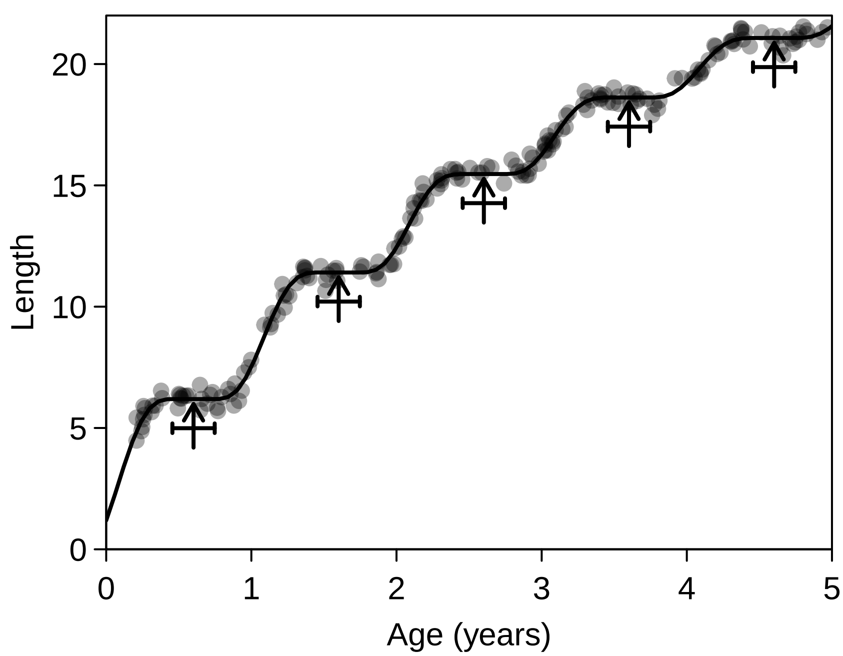

Figure 3: Example VBGF using Equation 4 with L_∞=30, $K^{'}$=0.35, t_0=-0.1, NGT=0.2, t_s=0.1 (with WP=0.55) and σ=0.3. Parameter estimates (and 95% confidence intervals) are shown in the first row of Table 1. Each WP is shown by the vertical arrow and each no-growth period is shown by the horizontal interval bar centered on the WP arrow.

Table 1: Parameter estimates from fitting Equation 5 to simulated data sets using L_∞=30, K'=0.35, t_0=-0.1, and varying values of t_s, NGT, and σ.

	tsset	NGTset	sigmaset	tsest	tslci	tsuci	NGTest	NGTlci	NGTuci	Linfest
[1,]	0.1	0.2	0.3	0.10	0.09	0.11	0.29	0.25	0.33	29.6
[2,]	0.1	0.2	0.5	0.10	0.09	0.12	0.19	0.12	0.26	30.1
[3,]	0.1	0.4	0.3	0.11	0.10	0.12	0.39	0.34	0.44	29.5
[4,]	0.1	0.4	0.5	0.10	0.08	0.12	0.38	0.30	NA	31.0
[5,]	0.5	0.2	0.3	0.51	0.50	0.52	0.15	0.10	0.19	30.0
[6,]	0.5	0.2	0.5	0.50	0.48	0.52	0.14	0.06	0.23	30.0
[7,]	0.5	0.4	0.3	0.49	0.48	0.50	0.41	0.36	0.46	31.2
[8,]	0.5	0.4	0.5	0.51	0.49	0.52	0.44	0.36	0.52	30.5

	Linflci	Linfuci	Kprest	Kprlci	Kpruci	t0est	t0lci	t0uci
[1,]	28.9	30.5	0.36	0.33	0.39	-0.09	-0.13	-0.06
[2,]	29.1	31.3	0.35	0.31	0.40	-0.08	-0.13	-0.04
[3,]	28.4	NA	0.35	0.32	0.40	-0.09	NA	-0.05
[4,]	29.0	33.6	0.32	0.26	0.39	-0.27	-0.39	-0.06
[5,]	29.4	30.5	0.33	0.31	0.35	-0.13	-0.16	-0.10
[6,]	29.1	31.1	0.33	0.29	0.37	-0.14	-0.20	-0.08
[7,]	30.1	32.3	0.34	0.30	0.37	-0.10	-0.15	-0.05
[8,]	29.1	32.3	0.37	0.31	0.43	-0.06	-0.14	0.02

Real Data

Stewart et al. (2013) examined the growth of 215 Bonito (*Sarda australis*) sampled from commercial landings. Fork lengths (mm) were measured for each fish and decimal ages were recorded as the number of opaque zones observed on otolith thin sections plus the proportion of the year after the designated birthdate (see Stewart et al. (2013) for more detailed methods). Stewart et al. (2013) fit Equation 3 to these data but constrained C to not exceed 1. Their model fit resulted in the boundary condition of $C = 1$, which suggested that Bonito ceased to grow at *at least* one point. This result suggests that Equation 5 should be fit to these data to determine the length of the no-growth period (Pauly et al. 1992).

Equation 4 fit the Bonito data slightly better than Equation 3 with slightly lower residual sums-of-squares (RSS) and Akaike Information Criterion (AIC) values. The length of the no-growth period was estimated to be 0.133 or 13.3% of the year. The t_s parameters were equal, the L_∞ parameters were similar, but the t_0 parameters differed somewhat between the two models. Finally, K from Equation 3 was equal to K' from Equation 5 multiplied by $1 - NGT$.

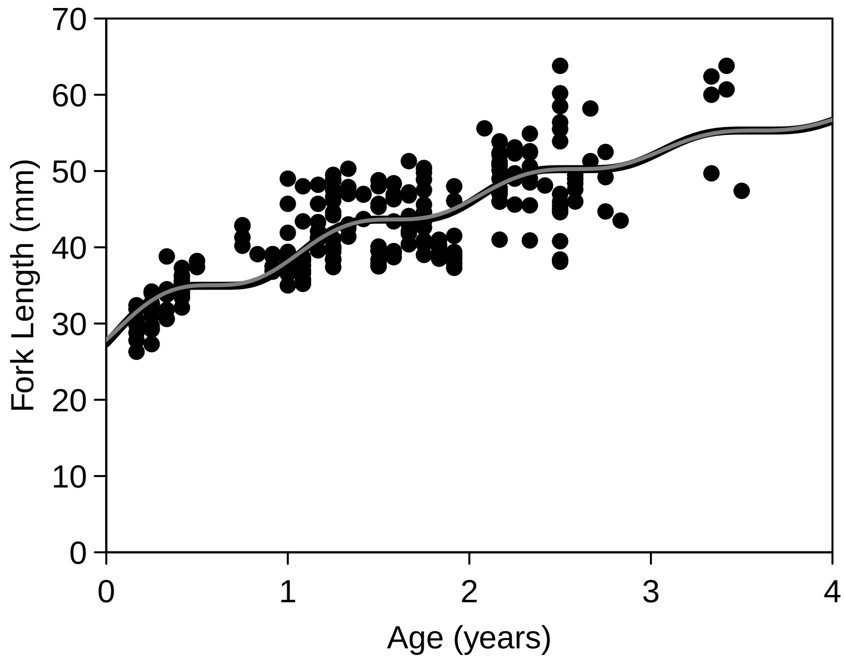

Figure 4: Fork length at age for Australian Bonito with the best-fit of Equation 5 (black line) and Equation 3 (gray line) superimposed. The parameter estimates (and 95% confidence intervals) from the model fits are shown in Table 2.

Table 2: Parameter estimates, residual sums-of-squares (RSS), and Akaike Information Criterion (AIC) from the fits of Equation 3 and Equation 5 to the Bonito data.

Somers Model (Equation 3) fit

	Est	2.5%	97.5%
Linf	71.86	58.53	230.11
K	0.27	0.04	0.51
t0	-1.92	-	-0.75
C	1.00	-	-
ts	0.09	-	0.18
RSS	4274.05	-	-
AIC	1435.86	-	-

Modified Pauly Model (Equation 6) fit

	Est	2.5%	97.5%
Linf	71.68	58.46	223.03
Kpr	0.31	0.05	0.66
t0	-1.64	-	-
ts	0.09	-	0.18
NGT	0.13	-	0.40
RSS	4265.70	-	-
AIC	1435.37	-	-

Discussion

- General
  - Fits perfectly simulated data well.
  - Parameters from real data seem reasonable
  - Other parameters by maths – WP=ts+0.5, SNG=WP-NGT/2, K=Kpr*(1-NGT)
  - Little practical difference between Equations 3 and 5 unless C>>1 and NGT>>0
- Model-Fitting
  - Fit Equation 3 first to see if C>=1
  - Problems due to 5 parameters
  - Bound parameters
- Assumptions
  - ts same time each year and age
  - NGT same length each year and age

Appendices

Appendix 1

```
################################################################################
## internal function to compute t-prime
################################################################################
iCalc_tpr <- function(t,ts,NGT) {
  ## Step 1
  SNG <- ts+(1-NGT)/2
  tmp.t <- t-SNG
  ## Step 2 (in parentheses) and Step 3
  tmp.t2 <- (tmp.t-floor(tmp.t))-NGT
  ## Step 4
  tmp.t2[tmp.t2<0] <- 0
  ## Step 5 (in parentheses) and Step 6 (also returns value)
  (floor(tmp.t)*(1-NGT)+tmp.t2) + SNG
}
```

Appendix 2

```
################################################################################
## Main Function
##   Linf, t0 as usual
##   Kpr = K-prime as defined in Pauly et al. (units are diff than usual K)
##   ts = start of sinusoidal growth (maximum growth rate)
##   NGT = "No Growth Time" = "fraction of a year where no growth occurs"
##   tpr = "t-prime" = actual age (t) minus cumulative NGT prior to t
################################################################################

VBSCGF <- function(t,Linf,Kpr=NULL,t0=NULL,ts=NULL,NGT=NULL) {
  if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]
  ts <- Linf[[4]]; NGT <- Linf[[5]]
  Linf <- Linf[[1]] }
```

```
  tpr <- iCalc_tpr(t,ts,NGT)
  q <- Kpr*(tpr-t0) +
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(tpr-ts)) -
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(t0-ts))
  Linf*(1-exp(-q))
}
```

References

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Page 533. United Kingdom Ministry of Agriculture; Fisheries.

Garcia-Berthou, E., G. Carmona-Catot, R. Merciai, and D. H. Ogle. 2012. A technical note on seasonal growth models. Reviews in Fish Biology and Fisheries 22:635–640.

Hoenig, N., and R. Choudaray Hanumara. 1982. A statistical study of a seasonal growth model for fishes. Tehcnical Report, Department of Computer Sciences; Statistics, University of Rhode Island.

Pauly, D., M. Soriano-Bartz, J. Moreau, and A. Jarre-Teichmann. 1992. A new model accounting for seasonal cessation of growth in fishes. Australian Journal of Marine and Freshwater Research 43:1151–1156.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing, v3.3.0. R Foundation for Statistical Computing, Vienna, Austria.

Schnute, J., and D. Fournier. 1980. A new approach to length-frequency analysis: Growth structure. Canadian Journal of Fisheries and Aquatic Sciences 37:1337–1351.

Somers, I. F. 1988. On a seasonally oscillating growth function. Fishbyte 6(1):8–11.

Stewart, J., W. Robbins, K. Rowling, A. Hegarty, and A. Gould. 2013. A multifaceted approach to modelling growth of the Australian bonito, *Sarda australis* (Family Scombridae), with some observations on its reproductive biology. Marine and Freshwater Research 64:671–678.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.